## CHARACTER SIGNIFICANCE AND GENERIC SIMILARITIES IN THE PANICEAE (POACEAE: PANICOIDEAE)

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#### ABSTRACT

A comprehensive study of character significance and generic similarity is presented for genera of the Paniceae. A computerized database consisting of 102 recognized genera recorded 285 characters was constructed and analyzed by the DELTA system. The minimum combination of significant characters required to distinguish each genus within the Paniceae is given in form of diagnostic descriptions. Distribution and use of characters within the diagnosis are discussed. Presence of shared significant characteristics are used to defined generic groups. Morphological similarities among genera within the groups are fully analyzed.

INTRODUCTION

One hundred two (102) genera are recognized in this taxonomic study of the

Paniceae R. Br. of the world. The Paniceae is defined here in a broad sense and includes genera placed in apparently closely related or similar tribes such as the Neurachneae Blake, Isachneae Benth., and Melinideae Hitchc. Recognition of the 102 genera is based on studies by Webster (1987, 1988), Webster & Valdez (1988), Webster et al. (1989), and Webster (1991) who presented taxonomic treatments, primarily consisting of keys and descriptions for the Paniceae genera of the world. Recognition of some of the geographically restricted old world genera was based on concepts outlined by Clayton & Renvoise (1986) and Watson & Dallwitz (1988). Objectives of the present paper are to analyze taxonomic significance and distribution of characters in defining genera of the Paniceae and to discuss morphological similarities among recognized genera. The tribe encompasses approximately 2050 species geographically centered in the tropics and subtropics. Average number of species per genus is 20. Panicum (500 species), Paspalum (350), and Digitaria (250) encompass approximately 1100 species. Axonopus, Urochloa (including those species commonly placed in Bracharia), Setaria, Isachne, and Pennisetum have about 100 species each for a total of 500. These eight genera account for 73% of the species. Approximately 550 species occur in the remaining 94 genera. Average number of species per genus in this group is 5.9. Eleven genera (Paspalidium, Echinochloa, Ichnanthus, Eriochloa, Sacciolepis, Mesosetum, Cenchrus, Lasiacis, Poecilostachys, Thrasya, and Acroceras) have

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20 - 40 species. Twenty-one genera have 5 - 15 species. Two to four species are found in 25 genera, and 37 of the 102 genera are monotypic.

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Approximately one-half of the genera are geographically restricted to a single continent. *Amphicarpum* is endemic to North America. *Ixophorus, Reynaudia, Scutachne*, and *Triscenia* occur only in Mesoamerica. Eight genera including Anthaenantiopsis, Centrochloa, Oplismenopsis, Otachyrium, Plagiantha, Spheneria, Tatianyx, and Thrasyopsis are endemic to South America. Twenty-four genera (Acritochaete, Baptorbachis, Chaetopoa, Chlorocalymma, Cyphochlaena, Eccoptocarpha Heteranthoecia, Holcolemma, Hydrothauma, Hylebates, Lecomtella, Louisiella, Megaloprotachne, Microcalamus, Mildbraediochloa, Odontelytrum, Oryzidium, Poecilostachys, Snowdenia, Stereochlaena, Streptolophus, Tarigidia, Thyridachne, and Yvesia) occur only in Africa. Asia has three endemic genera (*Limnopoa, Sphaerocaryum*, and *Trachys*). Fifteen genera (*Arthragrostis, Calyptochloa, Chamaeraphis, Homopholis, Uranthoecium, Whiteochloa, Xerochloa, Yakirra* and Zygochloa) occur only in Australia. Finally, one genus, *Dissochondrus*, is endemic to the Pacific Islands. Of the 56 genera mentioned in this paragraph, 37 are monotypic and 12 have 2–3 species.

#### MATERIALS AND METHODS

As in my other publications on genera of the Paniceae, the DELTA system (Dallwitz 1974, 1980) is used in the collection, analysis, and interrogation of taxonomic database. A complete and original set of data was collected for 285 characters for 102 recognized genera. The character list, published on microfiche in Webster (1989), consists of an ordered sequence of characters required for describing and identifying all subtribal categories. Taxonomic data for all characters were gathered based on original studies of specimens for the species of each genus. For most genera, specimens for all species were studied for the collections of data; however, for the larger genera (eg. Panicum and Paspalum) specimens from representative species were used. The number of specimens used for each species varied. Data in DELTA format were converted to INTKEY format for the generic analysis presented in this paper. INTKEY is specifically designed for information retrieval and database interrogation. For this analysis characters are weighted relative to how reliable the character is in discriminating among the taxa. Assessment of reliability is based on the degree of consistency within a genus and on how well the character can be applied. For example, if a character is easy to determine and totally consistent within a genus then it is considered to be more reliable than a character difficult to determine and variable among the species of the genus. This weight and the effectiveness of the characters in separating taxa into equal groups were important parameters influencing the following analysis. Additional specific methods are given with each of the following sections.

#### DIAGNOSTIC DESCRIPTIONS AND CHARACTER SIGNIFICANCE

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The following are diagnostic descriptions for the genera. They are diagnostic in that they contain the minimum number of important characters required to separate the genus from all others of the group. For example, the combination of four character states found in the description of Acritochaete are unique to that genus. Selection of characters by INTKEY is influenced by variation in other genera and by my concept of character reliability. For example, point of disarticulation is weighted high as a taxonomically reliable character and would be selected over a lower weighted character, even though they may have similar separating power. Thirty-nine of the available 285 characters are used in diagnostic descriptions of 102 recognized genera. The more variable a genus is for highly reliable characters the more characters are required for separation. Number of characters required for each genus varied from 2 (eg. Cleistochloa and Eriochloa) to 14 in Panicum. Other genera requiring a relatively high number of characters are Acroceras and Hymenachne. An explanation and definition of the terminology used in the following descriptions is given in Webster (1988 & 1989); however, a brief discussion of the terms rachis and quaquaversal seems appropriate. Rachis is used to specify the axis from which the spikelets or spikelet clusters originate. For example, the main axis becomes the rachis when the inflorescence is a spike or raceme. The rachis of a panicle may be either the primary branches or the secondary branches, depending on the degree of branching. Quaquaversal is a type of branching pattern where the branches may originate from any point on the axis. This is in opposition to secund, where the branches originate on one side of the axis, and distichous, where branches originate from two opposite sides of the axis.

## Diagnostic Descriptions

1. Acritochaete Pilger—Ligule a membrane. Main axis with secund primary branches. Pedicels oblique to the spikelet base. Disarticulation at the spikelet base.

2. Acroceras Stapf—Ligule a membrane or a ciliate membrane. Inflorescence a panicle. Rachis terminating in a spikelet. Pedicels truncate at the apex; concave. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Spikelets adaxial; dorsiventrally compressed. Second glume rounded on the back. Lemma of upper floret indurate; glabrous; muticous or apiculate.

3. Alloteropsis Presl—Spikelets abaxial. Lemma of lower floret with a hyaline area at the base. Lemma of upper floret awned.

4. Amphicarpum Kunth—Cleistogamous inflorescence present. Spike-lets heteromorphic.

5. Ancistrachne S.T. Blake—Ligule a ciliate membrane. Primary branches with distichous spikelets. Lemma of upper floret smooth; mucronate.

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6. Anthaenantia P. Beauv.—Inflorescence a panicle. Primary branches with spreading secondary branches. Disarticulation at the spikelet base). First glume absent. Lemma of upper floret chartaceous; muticous.

7. Anthaenantiopsis Pilger—Ligule a ciliate membrane or a fringe of hairs. Inflorescence a panicle. Main axis with distichous primary branches. Pedicels flat. Disarticulation at the spikelet base.

8. Anthephora Schreb.—Primary branches reduced to a fascicle of spike-

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lets. Rachis terminating in a spikelet. Disarticulation at the base of the primary branches.

9. Arthragrostis Lazarides—Ligule a ciliate membrane. Primary branches with spreading secondary branches. Rachis terminating in a spikelet. Spikelets abaxial. Rachilla pronounced between the florets.

10. Arthropogon Nees—Inflorescence a panicle or a raceme. Disarticulation at the spikelet base. Callus differentiated. Spikelets laterally compressed. First glume awned. Lemma of upper floret muticous.

11. Axonopus P. Beauv.—Inflorescence a panicle. Primary branches with appressed secondary branches. Rachis terminating in a spikelet. Pedicels concave. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Spikelets adaxial. First glume absent. Second glume rounded on the back. Lemma of upper floret muticous.

12. Baptorhachis Clayton & Renvoise—Ligule a ciliate membrane. Inflorescence a raceme. First glume absent.

13 Brachiaria (Trin.) Griseb.—Main axis with secund primary branches. Rachis terminating in a spikelet. Spikelets planoconvex. Lemma of upper floret chartaceous; smooth; muticous.

14. CalyptochloaC.E. Hubb.—Cleistogamous inflorescence present. Lemma of upper floret awned.

15. Cenchrus L.—Ligule a ciliate membrane or a fringe of hairs. Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Callus flared to form a discoid receptacle. Cleistogamous inflorescence absent. Lemma of upper floret muticous.

16. Centrochloa Swallen—Ligule a ciliate membrane. Pedicels convex. Disarticulation at the spikelet base. Callus differentiated.

17. Chaetium Nees-Ligule a fringe of hairs. Pedicels oblique to the

spikelet base. Lemma of upper floret mucronate to awned.

18. Chaetopoa C.E. Hubb.—Disarticulation at the base of the primary branches. First glume awned. Lemma of upper floret mucronate.

19. Chamaeraphis R. Br.—Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Spikelets planoconvex to terete.

20. Chlorocalymma Clayton—Ligule a membrane. Primary branches reduced to a fascicle of spikelets. Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Callus differentiated.

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21. Cleistochloa C.E. Hubb.—Cleistogamous inflorescence present. Lemma of upper floret muricate.

22. Coelachne R. Br.—Rachis terminating in a spikelet. Fertile florets 2. Lemma of lower floret membranous.

23. Cyphochlaena Hack.—Main axis with secund primary branches. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets heteromorphic.

24. Cyrtococcum Stapf-Ligule a membrane. Main axis with quaquaversal primary branches. Disarticulation at the spikelet base. Spikelets laterally compressed. Second glume rounded on the back.

25. Digitaria Haller-Ligule a membrane or a ciliate membrane. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets abaxial; planoconvex. Second glume rounded on the back. Lemma of upper floret with flat margins; glabrous; muticous or mucronate.

26. Dissochondrus (Hillebr.) Kuntze-Rachis terminating in a bristle. Fertile florets 2.

27. Eccoptocarpha Launert—Ligule a fringe of hairs. Disarticulation at the spikelet base. Second glume slightly saccate.

28. Echinochloa P. Beauv.—Ligule a fringe of hairs or absent. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. First glume encircling the spikelet base. Rachilla not pronounced between the florets. Second glume rounded on the back. Lemma of upper floret indurate; smooth; glabrous; muticous.

29. Echinolaena Desv.-Ligule a ciliate membrane or a fringe of hairs. Rachis terminating in a spikelet. Pedicels flat to convex. Disarticulation at the spikelet base. Rachilla pronounced between the florets. Lemma of upper floret muticous.

30. Entolasia Stapf—Ligule a fringe of hairs. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Rachilla not pronounced below the second glume. Lemma of upper floret hairy.

31. Eriochloa Kunth—First glume fused with the callus to form a cuplike structure. Lemma of upper floret mucronate or awned.

32. Heteranthoecia Stapf—Rachis terminating in a spikelet. Fertile florets 2. Lemma of lower floret chartaceous.

33. Holcolemma Stapf & C. E. Hubb.-Ligule a membrane. Disarticulation at the spikelet base. First glume inflated at the base. Second glume rounded on the back. Lemma of lower floret with the area between the central nerve and the first lateral nerve thinner in texture than the rest of the structure.

34. Homolepis Chase—Ligule a membrane. Primary branches with spreading secondary branches. Disarticulation at the spikelet base. Lemma of upper floret chartaceous to coriaceus; with flat margins.

35. Homopholis C.E. Hubb.—Ligule a membrane. Inflorescence a panicle.

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Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets abaxial; laterally compressed to dorsiventrally compressed. Second glume rounded on the back. Lemma of lower floret consistent in texture. Lemma of upper floret with flat margins; muticous or mucronate.

36. HydrothaumaC.E. Hubb.—Ligulea membrane. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets abaxial. Lemma of lower floret consistent in texture. Lemma of upper floret

chartaceous; muticous.

37. Hygrochloa Lazarides—Plants monoecious. Spikelets heteromorphic. 38. Hylebates L. Chippindall—Ligule a ciliate membrane. Inflorescence a panicle. Primary branches with spreading secondary branches. Rachis terminating in a spikelet. Spikelets dorsiventrally compressed. First glume present; not encircling the spikelet base. Lemma of upper floret muticous.

39. Hymenachne P. Beauv.—Ligule a membrane or a ciliate membrane. Inflorescence a panicle. Primary branches with appressed secondary branches. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Spikelets adaxial. First glume encircling the spikelet base. Second glume rounded on the back. Lemma of upper floret membranous to chartaceous; with flat margins; glabrous; muticous.

40. Ichnanthus P. Beauv.—Inflorescence a panicle. Rachis terminating in a spikelet. Pedicels concave. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. First glume encircling the spikelet base. Rachilla pronounced between the florets. Second glume rounded on the back. Lemma of upper floret glabrous; with basal scars or appendages; muticous.

41. Isachne R. Br.—Rachis terminating in a spikelet. Fertile florets typically 2. Lemma of lower floret cartilaginous.

42. Ixophorus Schlecht.—Ligule a membrane. Rachis terminating in a bristle. Lemma of upper floret mucronate.

43. Lasiacis (Griseb.) Hitchc.—Ligule a membrane. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets terete.

44. Lecomtella A. Camus—Plants and romonoecious. Inflorescence a panicle. Rachis terminating in a spikelet.

45. Limnopoa C.E. Hubb.—Inflorescence a raceme. Disarticulation above the lower glume.

46. Louisiella C.E. Hubb. & Leonard—Ligule a ciliate membrane. Inflorescence a panicle. Main axis with quaquaversal primary branches. Rachis terminating in a spikelet. Disarticulation at the spikelet base. First glume not encircling the spikelet base. Lemma of upper floret chartaceous; with involute margins; muticous.

47. Megaloprotachne C.E. Hubb.—Spikelets planoconvex. Lemma of upper floret apiculate.

48. Melinis P. Beauv.—Ligule a fringe of hairs. Inflorescence a panicle. Main

axis with quaquaversal primary branches. Primary branches with spreading secondary branches; with spikelets neither secund nor distichous. Disarticulation at the spikelet base. Callus not differentiated. Spikelets laterally compressed. First glume present. Lemma of upper floret hyaline to membranous.

49. Mesosetum Steud.—Inflorescence a raceme. Pedicels oblique to the spikelet base. Spikelets adaxial.

50. Microcalamus Franch.—Ligule a ciliate membrane. Rachis terminating in a spikelet. Rachilla pronounced between the florets. Lemma of upper floret indurate; with flat margins; muticous.

51. Mildbraediochloa Butzin—Spikelets laterally compressed. Lemma of upper floret awned.

52. Neurachne R. Br.—Inflorescence a raceme. Disarticulation at the spikelet base. Callus differentiated. Spikelets abaxial. Lemma of upper floret hyaline to membranous.

53. Odontelytrum Hack.—Ligule a membrane. Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Callus not differentiated. Spikelets adaxial.

54. Oplismenopsis Parodi-Ligule a ciliate membrane. Inflorescence a panicle. Primary branches with appressed secondary branches. Rachis terminating in a spikelet. Pedicels concave. Disarticulation at the spikelet base. Callus not differentiated. First glume awned. Lemma of upper floret muticous. 55. Oplismenus P. Beauv.—Main axis with secund primary branches. First glume awned. Lemma of upper floret mucronate. 56. Oryzidium C.E. Hubb. & Schweick.—Ligule a fringe of hairs. Inflorescence a panicle. Main axis with quaquaversal primary branches. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Rachilla pronounced between the florets. Lemma of upper floret chartaceous; glabrous; muticous. 57. Otachyrium Nees—Ligule a membrane or a ciliate membrane. Inflorescence a panicle. Main axis with quaquaversal primary branches. Rachis terminating in a spikelet. Pedicels concave. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Second glume gibbose or rounded on the back. Lemma of lower floret with a hyaline area at the base. Lemma of upper floret glabrous; muticous.

58. Ottochloa Dandy—Ligule a ciliate membrane. Lemma of upper floret muricate; with involute margins; mucronate.

59. Panicum L.—Ligule a membrane or a ciliate membrane. Inflorescence a panicle. Rachis terminating in a spikelet. Pedicels cupuliform at the apex; concave. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Spikelets adaxial; dorsiventrally compressed. Rachilla pronounced between the florets or not pronounced between the florets. Second glume rounded on the back. Lemma of upper floret cartilaginous; glabrous; muticous.

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60. Paractaenum P. Beauv.—Main axis with distichous primary branches. Disarticulation at the base of the primary branches. Lemma of upper floret cartilaginous.

61. Paraneurachne S.T. Blake—Inflorescence a raceme. Pedicels oblique to the spikelet base. Lemma of upper floret indurate.

62. Paratheria Griseb.—Disarticulation at the base of the primary branches. Cleistogamous inflorescence present.

63. Paspalidium Stapf—Main axis with distichous primary branches or with secund primary branches. Rachis terminating in a bristle. Disarticulation at the spikelet base.

64. **Paspalum** L.—Pedicels flat or convex. Disarticulation at the spikelet base. Spikelets planoconvex. Lemma of upper floret indurate; smooth or striate; muticous.

65. Pennisetum Rich.—Ligule a ciliate membrane or a fringe of hairs. Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Callus not flared to form a discoid receptacle. Cleistogamous inflorescence absent. Lemma of upper floret muticous.

66. Plagiantha Renv.—Ligule a ciliate membrane. Inflorescence a panicle.
Primary branches with spreading secondary branches. Disarticulation at the spikelet base. Lemma of lower floret membranous; with a central longitudinal groove.
67. Poecilostachys Hack.—Ligule a membrane. Main axis with secund primary branches. Disarticulation at the spikelet base. Spikelets adaxial; laterally compressed.

68. PseudechinolaenaStapf—Spikelets laterally compressed. Second glume gibbose.

69. Pseudochaetochloa Hitchc.—Plants andromonoecious. Lemma of upper floret mucronate.

70. **Pseudoraphis** Griff.—Inflorescence a panicle or a raceme. Rachis terminating in an unmodified naked point. Disarticulation at the spikelet base or at the base of the primary branches. Rachilla pronounced between the florets.

71. Reimarochloa Hitchc.—Second glume absent. Disarticulation at the base of the primary branches.

72. Reynaudia Kunth—Ligule a fringe of hairs. Inflorescence a panicle. Disarticulation at the spikelet base. Spikelets laterally compressed. First glume awned. Second glume rounded on the back. Lemma of upper floret muticous. Stamens 2.

73. Rhynchelytrum Nees—Ligule a fringe of hairs. Inflorescence a panicle. Main axis with secund primary branches. Disarticulation at the spikelet base. Spikelets laterally compressed.

74. Sacciolepis Nash—Second glume saccate. Lemma of upper floret scabrous.

75. Scutachne Hitchc. & Chase—Ligule a fringe of hairs. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. First glume encircling the spikelet base. Second glume rounded on the back. Lemma of upper floret with flat margins; glabrous; muticous. Palea of upper floret not enclosed at the apex.

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76. Setaria P. Beauv.—Main axis with quaquaversal primary branches. Rachis terminating in a bristle. Disarticulation at the spikelet base. Fertile florets 1. Lemma of lower floret consistent in texture. Lemma of upper floret muticous. 77. Setariopsis Scribn. & Millsp.—Rachis terminating in a bristle. Disarticulation at the spikelet base. Lemma of lower floret with a hyaline area at the base.

78. Snowdenia C.E. Hubb.-Inflorescence a raceme. Pedicels convex. Lemma of upper floret membranous.

79. Sphaerocaryum Hook. f.—Inflorescence a panicle. Disarticulation above the lower glume. Fertile florets 1. Lemma of upper floret hairy.

80. Spheneria Kuhlm.—Ligule a membrane. Main axis with distichous primary branches. Pedicels oblique to the spikelet base. Disarticulation at the spikelet base.

81. Spinifex L.—Flowering culms with inflorescences densely clustered in a spatheate panicle. Inflorescence a raceme or a spike.

82. Stenotaphrum Trin.—Ligule a ciliate membrane. Disarticulation at the nodes of the main axis or at the base of the inflorescence.

83. Stereochlaena Hack.—Ligule a ciliate membrane. Inflorescence a panicle. Spikelets planoconvex. Lemma of upper floret chartaceous; minutely muricate; muticous.

84. Streptolophus Hughes—Ligule a membrane. Rachis terminating in a bristle. Disarticulation at the base of the primary branches. Lemma of upper floret muricate.

85. Streptostachys Desv.—Ligule a fringe of hairs or absent. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. Lemma of upper floret indurate; hairy.

86. Tarigidia Stent—Main axis with quaquaversal primary branches. Rachis terminating in a spikelet. Disarticulation at the base of the primary branches. Spikelets planoconvex. Second glume present.

87. Tatianyx Zuloaga & Soderstrom-Inflorescence a panicle. Pedicels oblique to the spikelet base. Disarticulation at the spikelet base. Lemma of lower floret with a hyaline area at the base. Lemma of upper floret muticous.

88. Thrasya Kunth—Ligule a membrane. Main axis with secund primary branches. Lemma of lower floret membranous; with a hyaline area at the base or with the area between the central nerve and the first lateral nerve thinner in texture than the rest of the structure.

89. Thrasyopsis Parodi—Ligule a membrane and a fringe of hairs. Inflores-

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cence a panicle. Pedicels flat. Disarticulation at the spikelet base. Lemma of lower floret cartilaginous to indurate. Lemma of upper floret glabrous; muticous. 90. Thuarea Pers.—Plants monoecious or andromonoecious. Disarticulation at the base of the inflorescence.

91. Thyridachne C.E. Hubb.—Ligule a membrane. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Spikelets abaxial. First glume encircling the spikelet base. Lemma of lower floret with the area between the central nerve and the first lateral nerve thinner in texture than the rest of the structure.

92. Thyridolepis S.T. Blake-Ligule a fringe of hairs. Inflorescence a raceme. Spikelets planoconvex. Lemma of upper floret chartaceous to cartilaginous.

93. Triscenia Griseb.—Inflorescence a panicle. Main axis with distichous primary branches. Disarticulation at the spikelet base. Spikelets adaxial. Lemma of upper floret hyaline to membranous.

94. Trachys Pers.—Rachis terminating in a spikelet. Disarticulation at the nodes of the main axis or at the nodes of the primary branches.

95. Tricholaena Schult.—Inflorescence a panicle. Main axis with distichous primary branches or with secund primary branches. Primary branches with spreading secondary branches. Rachis terminating in a spikelet. Callus minutely differentiated. Spikelets dorsiventrally compressed.

96. Uranthoecium Stapf-Disarticulation at the nodes of the main axis. Lemma of upper floret awned.

97. Urochloa P. Beauv.—Ligule a fringe of hairs. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. First glume not fused with the callus. Rachilla not pronounced between the florets. Second glume rounded on the back. Lemma of upper floret rugose; with involute margins; glabrous.

98. Whiteochloa C.E. Hubb.-Plants dioecious. Rachis terminating in a spikelet.

99. Xerochloa R. Br.—Flowering culms with inflorescences in a spatheate raceme. Inflorescence a spike or a solitary spikelet.

100. Yakirra Lazarides & R. Webster-Plants hermaphroditic. Ligule a fringe of hairs. Inflorescence a panicle. Rachis terminating in a spikelet. Disarticulation above the lower glume or at the spikelet base. Cleistogamous inflorescence absent. Rachilla pronounced between the florets. Fertile florets 1. Lemma of upper floret indurate; glabrous; muticous. 101. Yvesia A. Camus-Ligule a fringe of hairs. Rachis terminating in a spikelet. Disarticulation at the spikelet base. Cleistogamous inflorescence absent. First glume not fused with the callus; absent. Lemma of upper floret mucronate. 102. Zygochloa S.T. Blake—Plants dioecious. Inflorescence a solitary spikelet.

## Character Significance

An assessment of character significance is based on how well a character separates among the taxa and its importance for identification of the taxa. For example, a character which does not appear in the diagnostic descriptions would be considered insignificant relative to one appearing numerous times. Furthermore, a character appearing in a relatively high percentage of the descriptions would be considered more significant than one appearing in a low percentage.

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The following paragraphs present a discussion of the significance of characters and the distribution of the character states for the taxa.

Plant sexuality (hermaphroditic, dioecious, etc.) is required for identification of seven genera (Hygrochloa, Lecomtella, Pseudochaetochloa, Thuarea, Whiteochloa, Yakirra and Zygochloa). Only two characters related to vegetative features of the plant are used in the results. The first relates to the branching pattern subtending the inflorescences. In Spinifex, culms are branched forming a spatheate panicle and in Xerochloa the branching forms a spatheate raceme. The second vegetative characteristic is whether the ligule is a membrane, ciliate membrane, fringe of hairs, or absent. This character is required in 51 of the descriptions. A membrane is exclusively found in 21 genera and a fringed membrane in 18 genera. A fringe of hairs is characteristic of 36 and the ligule absent only in Echinochloa. Eleven characters of the inflorescence are used for identification of the genera. Type of inflorescence (panicle, raceme, spike, or solitary) is used in 43 descriptions. Most genera possess some variation of panicle. However, nine genera (Baptorhachis, Calyptochloa, Limnopoa, Mesosetum, Neurachne, Paraneurachne, Snowdenia, Thuarea, Thyridolepis) have only racemes and one genus, Zygochloa, is described as having a solitary spikelet as the inflorescence. No genus is characterized as having only a spike inflorescence. Arrangement of primary branches on the main axis of the inflorescence (distichous, secund, or quaquaversal) is of diagnostic importance in 20 genera. The quaquaversal arrangement is most common but distichous or secund primary branches are found in 28 taxa. Whether secondary inflorescence branches are appressed, spreading or reduced to a fascicle of spikelets was used in 12 descriptions. Approximately one-half of the genera have exclusively appressed secondary branches, whereas 13 genera are spreading only. Exclusive reduction of branches to a fascicle of spikelets is found in seven genera (Anthephora, Cenchrus, Chlorocalymma, Odontelytrum, Pennisetum, Streptolophus and Trachys). Arrangement of spikelets or secondary branches on primary branches (secund, distichous, and quaquaversal) is used in the descriptions of Ancistrachne and Melinis. This character has limited taxonomic value especially with the open inflorescence form. One of the most taxonomically significant characters of the Paniceae is presence or absence of bristles. This character appears in 46 descriptions. Seventy-six genera have spikelets terminat-

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ing the branches and 26 possess some variation of a bristle. Holcolemma and possibly Pseudochaetochloa are the only genera variable for this character. The pedicel apex has modifications which are taxonomically significant. Whether or not the pedicel apex is differentiated is significant and related to point of disarticulation. The pedicel apex is not differentiated in those genera where the primary point of disarticulation is not at the base of the spikelet. For example, in Cenchrus the pedicel apex cannot be comparatively described. For those genera commonly placed in the Isachneae, where disarticulation is above the glumes, the pedicel apex is not differentiated and clearly different from other genera of the Paniceae. Three characteristics of the pedicel apex are used in the descriptions. Shape of the pedicel apex (truncate, discoid and cupuliform) is taxonomically significant for the genera and especially within Digitaria; however, occasionally the states are difficult to determine. Thirteen genera are exclusively truncate (eg. Acroceras and Paspalum), 35 discoid (eg. Eriochloa and Setaria), and 22 cupuliform (eg. Panicum and Entolasia). The remaining 33 genera are variable for these states. Angle of disarticulation (perpendicular or oblique) with the axis of the pedicel is required in six descriptions. Acritochaete, Chaetium, Mesosetum, Paraneurachne, Spheneria, and Tatianyx are exclusively oblique at the pedicel apex, whereas the remaining genera have the typical perpendicular morphology. For taxa where the pedicel apex is differentiated, the apex can be concave, flat or convex. This character is used in 12 descriptions. As expected, the most common state is concave with 63 genera (eg. Panicum and Setaria). A flat pedicel apex is found exclusively in eight genera (eg. Oplismenus, Pseudoraphis), and two genera are exclusively convex (Centrochloa and Snowdenia). Echinolaena, Paspalum, Thrasya are flat to convex. This character is particularly useful for separating Paspalum from otherwise similar genera. Point of disarticulation occurs in 65 descriptions and is taxonomically the most reliable character within the Paniceae. Disarticulation is exclusively above the glumes only in the Isachneae. The most common state which is found in 69 genera is disarticulation exclusively at the spikelet base. Twelve genera disarticulate at the base of the primary branches of the inflorescence. Uranthoecium disarticulates at nodes of the main axis. Thuarea and Xerochloa disarticulate at the base of the inflorescence. No genera disarticulate exclusively at culm nodes; however, this state can occur in Calyptochloa, Spinifex and Zygochloa. Disarticulation at some point below the primary branches is restricted to genera occurring in Australia. Morphological differentiation at the point of disarticulation is referred to as the callus. This character occurs in eight descriptions. The callus is differentiated in 21 genera (see Cenchrus and Spheneria). Modifications of the callus include whether it is prolonged as in Centrochloa, flared as in Cenchrus, oblique as in Paratheria and Chaetium, or hairy as in Neurachne and Arthropogon. Relative length and color of the callus hairs has limited taxonomic significance.

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Presence of absence of cleistogamous inflorescences is used in 20 descriptions. The North American genus Amphicarpum and three Australian genera (Calyptochloa, Cleistochloa and Paratheria) possess cleistogamous inflorescences. Cleistogamous spikelets do occur in a number of other genera. In all four genera cleistogamous spikelets are morphologically different from chasmogomous spikelets. Amphicarpum is the only genus with a subterranean cleistogamous inflorescence.

Three general characters of the spikelets are included in the descriptions. Presence or absence of morphologically different spikelets was used in three descriptions. Truly heteromorphic spikelets are characteristic of Amphicarpum, Cyphochlaena and Hygrochloa. Orientation of spikelets to the flowering axis or rachis is required in 15 descriptions. Even though this character has significant evolutionary implications its taxonomic value is limited because it is frequently difficult or impossible to determine especially when the inflorescence is open with spreading secondary branches. This character is also difficult to determine when the rachis is modified producing a spikelet cluster as in Cenchrus. However, for many genera (eg. Digitaria and Paspalum) the character is very useful. The terms abaxial and adaxial are used to define whether the first glume or lemma of the lower floret is 180 degrees from the rachis or whether the first glume or lemma of the lower floret faces the rachis. Approximately 1/2 of the genera fall into each category. Spikelet compression is used in 22 descriptions and is generally a reliable character. The most common state is dorsiventrally compressed and exclusively found 56 genera. Lateral compression is found in 21 genera (eg. Melinis and Cyrtococcum). Twelve taxa including Baptorhachis, Brachiaria, Digitaria, Hygrochloa, Megaloprotachne, Paraneurachne, Paspalum, Reimarochloa, Stereochlaena, Tarigidia, Thyridolepis and Uranthoecium are exclusively planoconvex. Only one genus, Lasiacis, is recorded as exclusively terete. Five characteristics of the first glume are used in the descriptions. Presence or absence of the first glume is found in 6 descriptions. Eighty-one genera always possess a first glume. Complete absence of a first glume is characteristic of eight genera (Anthaenantia, Axonopus, Baptorhachis, Centrochloa, Reimarochloa, Spheneria, Tricholaena and Yvesia). Thirteen genera are variable for this character. Fusion of the first glume with the callus is characteristic of Eriochloa but also found to a limited degree in Thrasya. Significant fusion is not found in the remaining genera. Whether or not the first glume encircles the spikelet base is a significant character but rarely used by taxonomists. This character appears in seven descriptions. The first glume encircles the spikelet base in 36 genera (eg. Panicum and Echinochloa) and does not encircle the spikelet base in 55 genera (eg. Digitaria and Neurachne). The remaining 11 genera either lack the first glume or is variable for this character. Pronounced presence of an inflated base on the first glume is found in Holcolemma, Lasiacis and Setariopsis, but only used in the description of Holcolemma.

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The final characteristic of the first glume used in the diagnostic descriptions is whether an awn is present. An awned first glume is found exclusively in *Arthropogon, Chaetium, Chaetopoa, Cyphochlaena, Oplismenopsis, Oplismenus* and *Reynaudia*. This character is used in five of the descriptions. An awn is never found in 69 genera and variable in *Anthephora, Arthragrostis, Echinolaena, Mesosetum, Paraneurachne* and *Tarigidia*.

Whether the rachilla is pronounced between the glumes or between the florets occurs in 11 descriptions. A pronounced rachilla between the glumes is found exclusively in 19 genera (eg. *Hymenachne* and *Oryzidium*) and not found in 69 genera. It is variable for the remaining 14 genera. For example, in *Digitaria* section Trichachne (Stapf) Henrard this portion of the rachilla is present but not present in section *Digitaria*. The rachilla pronounced between florets is exclusively present in 15 genera (eg. *Ichnanthus* and *Eccoptocarpha*) and not found in 79. Additional modifications of the rachilla between the florets include whether it is straight (eg. *Limnopoa*) or geniculate (eg. *Ichnanthus*), whether it is filiform (eg. *Arthragrostis*) or swollen (eg. *Yakirra*), presence of lateral appendages (eg. *Ichnanthus*), and length of the rachilla (relatively long in *Oryzidium* and short in *Calyptochloa*).

Two characters of the second glume are used in the descriptions. Whether the second glume is present or absent is found in descriptions of *Tarigidia* and *Reimarochloa*, which is the only genus where the second glume is exclusively absent. The second glume is present or absent in the African genera, *Baptorhachis* and *Stereochlaena*. Whether the second glume is saccate, gibbose or simply rounded is found in 17 of the descriptions. A saccate second glume is exclusively found in *Eccoptocarpha* and *Sacciolepis*. A gibbose second glume is characteristic of *Pseudechinolaena*. The remaining genera are simply rounded on the back except for *Digitaria* which is variable due to variation found in section *Gibbosae* Henrard. The number of fertile florets is found in seven of the diagnostic descriptions and primarily included here due to the inclusion of the genera traditionally placed in the Isachneae. Most (96) of the genera possess only one fertile floret. Two female fertile florets are found in *Coelachne*, *Heteranthoecia* and *Isachne*. *Dissochondrus* is variable from 1 - 3 for this character.

Three characteristics of the lower floret are used in the descriptions. Texture of the lower lemma occurs in six descriptions. The most common texture for these genera is membranous, an exclusive characteristic of 56 genera. *Centrochloa*, *Chaetium*, *Megaloprotachne*, *Oryzidium*, *Reynaudia* and *Spheneria* possess a hyaline or membranous lemma, but only *Chaetopoa* is exclusively hyaline. Eight genera (*Heteranthoecia*, *Lasiacis*, *Otachyrium*, *Paraneurachne*, *Pseudechinolaena*, *Rhynchelytrum*, *Uranthoecium* and *Zygochloa*) are characterized by a chartaceous lower lemma. A cartilaginous or indurate lower lemma is found in 12 genera (eg. *Chamaeraphis*, *Setariopsis* and *Xerochloa*). Frequently, when the lower lemma is relatively thick in

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texture or the spikelets surrounded by protective structures the texture of the upper lemma is relative thin (see Cyphochlaena). Presence of a relatively thin area at the base of the lower lemma or a relatively thin central groove is a character used in 10 of the descriptions. Typical morphology for this character is the absence of these variations and found in 89 genera. A hyaline area at the base of the lower lemma occurs in nine taxa including Alloteropsis, Hygrochloa, Otachyrium, Pseudechinolaena, Setariopsis, Tatianyx, Thrasya, Whiteochloa and Xerochloa. A central relatively thin groove occurs in Holcolemma, Megaloprotachne, Mesosetum, Thrasya, Thrasyopsis, Thyridachne and Uranthoecium. These variations are frequently correlated with presence of well developed stamens in the lower floret. Six characters of the upper floret are used in the descriptions. Texture of the upper lemma occurs in 22 descriptions. The most common character state for the genera is chartilaginous to indurate which occurs in 63 genera. A hyaline upper lemma is found exclusively in Chaetopoa, Cyphochlaena, Mildbraediochloa and Reynaudia. A membranous upper lemma occurs exclusively in Chamaeraphis, Coelachne, Snowdenia and Sphaerocaryum. The remaining 32 genera are variable for this character. For example, six genera are membranous or chartaceous. Modification of the margins of the upper lemma occurs in nine descriptions. Forty-nine genera have flat margins and 47 possess involute margins. The remaining six genera (Alloteropsis, Axonopus, Calyptochloa, Pennisetum, Stenotaphrum and Uranthoecium) are variable for these states. Revolute or convolute margins are not found in the Paniceae. Whether the upper lemma is hairy or glabrous is used in 15 descriptions. The most typical state is glabrous which is exclusive for 89 genera. A hairy upper floret is exclusively found in Amphicarpum, Entolasia, Heteranthoecia, Limnopoa, Sphaerocaryum and Streptostachys. The following five genera are variable for this character (Cleistochloa, Coelachne, Isachne, Microcalamus and Thrasya). Surface ornamentation of the upper floret occurs in 10 descriptions. The most common state is smooth which occurs in 56 genera. Sacciolepis and Snowdenia have a scabrous upper lemma. Striate taxa include Hygrochloa, Tatianyx and Thyridolepis. Eight taxa (eg. Cleistochloa and Stereochlaena) are exclusively muricate. A pitted upper lemma does not occur in the Paniceae. Possibly the most taxonomically significant character state is whether the upper lemma is rugose or not. The following eight genera are exclusively rugose (Eriochloa, Holcolemma, Ixophorus, Paspalidium, Setaria, Setariopsis, Uranthoecium and Urochloa). The remaining 24 genera are variable for this character. For example, Digitaria is smooth, striate or muricate but never rugose. Presence of basal modification in the form of scars, appendages or constrictions is used only in the diagnostic description of Ichnanthus; however, Echinolaena has similar modifications at the base. Presence of an awned upper lemma is used in 43 descriptions. Ninety-three of the genera are unawned. Awned upper florets occur exclusively in Alloteropsis, Calyptochloa, Mildbraediochloa and Uranthoecium. Genera variable for this character

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include Acritochaete, Chaetium, Eriochloa, Snowdenia and Urochloa. Whether the apex of the upper palea is enclosed at the apex is used only in the diagnostic description of Scutachne, but also characteristic of Brachiaria and Anthaenantiopsis. The typical number of stamens for the genera is three. Two stamens is a characteristic of Reimarochloa, but may also be found in Reynaudia and Coelachne.

GENERIC SIMILARITIES

The objective of this section is to discuss morphological similarities among genera of the Paniceae as a mechanism of defining generic similaritites and generic concepts. To achieve this goal, it is advantageous to initially group together genera which have in common taxonomically significant characters. Once these initial groups are established the next most significant characters are used to define sub-groups or to isolate individual genera.

Whether the ultimate branches of the inflorescence terminates in a spikelet or bristle and point of disarticulation were the two characters shown to be most significant and reliable. These characters were initially used to separate among the genera. In the following lists of genera, numbers correspond to the generic numbers given with the diagnostic descriptions.

Cenchrus Group

15. Cenchrus 71. Reimarochloa 19. Chamaeraphis 81. Spinifex 20. Chlorocalymma 82. Stenotaphrum 53. Odontelytrum 84. Streptolophus 90. Thuarea 96. Uranthoecium 99. Xerochloa 102. Zygochloa

60. Paractaenum 62. Paratheria 65. Pennisetum 69. Pseudochaetochloa 70. Pseudoraphis

The Cenchrus group has in common the rachis terminating in a bristle and disarticulation at some point below the pedicel apex, usually at the base of the primary branches or at nodes of the main axis of the inflorescence. The most distinctive subgroup within this group are the Australia and Asia genera Spinifex, Xerochloa and Zygochloa. They have in common the inflorescences clustered in a spatheate raceme or panicle. Spinifex is unique in possessing a distinct bristle from 40 - 170 mm long, whereas the bristle in the other genera is much reduced. Xerochloa is the only genus with a spatheate raceme and thick spongy leaf blades. Zygochloa has an undeveloped callus and the upper floret lacks stamens. Of the remaining genera, Chamaeraphis, Paractaenum, Reimarochloa, Stenotaphrum and Uranthoecium have in common secund or distichous branching from the main axis

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of the inflorescence. Within this subgroup Chamaeraphis and Paractaenum, both from Australia, possess a differentiated callus and are best separated on texture of the upper floret. Presence of an awned upper floret distinguishes Uranthoecium, also from Australia, from this subgroup as does a hyaline modification on the lower lemma. The North American genus, Reimarochloa, is unique in the complete absence of the second glume. Stenotaphrum lacks the characters used to define other genera within this subgroup.

No character or combination of characters make a reasonable separation of the remainder of this group into unique morphologically similar subgroups. Pseudoraphis occurs here and also in the Setaria group due to its variation in point of disarticulation. It is most similar to taxa of the Setaria group. However, here it is unique in the presence of a pronounced rachilla between the florets. Cenchrus and Pennisetum are morphologically similar and overlap on most of the taxonomically important characters. The only reliable character concerns modification of the callus. In Cenchrus the callus apex is flared to form a receptacle for the spikelets, whereas in Pennisetum the callus is not flared. Chlorocalymma, a monotypic from Africa, has a series of unusual characteristics. Primary branches are broadly winged and enclose the spikelets, bristles are flattened and branched, and the lower lemma is winged. Odontelytrum, another African monotypic, lacks these characters but has in common with Chlorocalymma adaxial spikelets. A second glume less than 0.1 times spikelet length is the best character for distinguishing Paratheria. Pseudochaetochloa, an Australian monotypic, is the only dioecious genus of this group. Unique modifications of the branches of the primary branch in the form of hardened recurved spines serves to distinguish Streptolophus, an African monotypic. Thuarea, a monotypic from Asia and Australia, is morphologically similar to Stenotaphrum, however, it has adaxial and andromonecious spikelets.

## Setaria Group

26. Dissochondrus 33. Holcolemma 37. Hygrochloa 42. Ixophorus 52. Neurachne

69. Pseudochaetochloa 70. Pseudoraphis 76. Setaria 77. Setariopsis 88. Thrasya

#### 61. Paraneurachne 89. Thrasyopsis 63. Paspalidium 92. Thyridolepis

The Setaria group consists of 14 genera and possesses in common a rachis terminating in a bristle and disarticulation at the spikelet base. The most recognizable subgroup within this group is comprised of the Australian genera Thyridolepis, Neurachne and Paraneurachne. In this subgroup the inflorescence is a

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raceme and the ligule is a fringe of hairs. The first glume of *Thyridolepis* is unique within this subgroup and within the Paniceae in having a well-developed first glume with a transverse row of coarse seta subtended by a hyaline area. *Neurachne* has a smooth hyaline to membranous upper floret, whereas *Paraneurachne* has an indurate and muricate to rugose upper floret.

The remaining 11 genera of this group are best sub-divided into categories based on ornamentation of the lemma of the upper floret. Dissochondrus, Holcolemma, Setaria, Hygrochloa, Setariopsis, Ixophorus and Paspalidium have in common a rugose upper floret, whereas this structure in the remainder of the group is smooth to muricate. Dissochondrus in essentially identical to Setaria except for presence of more than one thickened fertile floret. The African genus Holcolemma is similar to Paspalidium and Setaria but has an inflated first glume and a central longitudinal groove on the lower lemma. Hygrochloa from Australia is the only monoecious genus of the group. The palea of the lower floret has pronounced wings in Holcolemma and Ixophorus. Ixophorus from Central America is best separated from Holcolemma on the basis of spreading primary inflorescence branches. Paspalidium is most similar to Setaria and distinguished on the basis of arrangement of the primary branches on the inflorescence. Setaria has quaquaversal primary inflorescence branches whereas Paspalidium has distichous or secund branching. Pseudochaetochloa, an Australian monotypic genus, is unique with and romonoecious sexuality. Pseudoraphis is the only member of this group with a pronounced rachilla between florets. Setariopsis, with two species from Central America, has a many-nerved second glume (13 - 23) and a hyaline area at the base of the lower lemma. Thrasya and Thrasyopsis are morphologically similar genera and the only members of this group with adaxial spikelets. These two genera are best separated on presence of a central groove on the lower lemma, number of nerves on the second glume, and texture of the lower floret.

## Anthephora Group

8. Anthephora
9. Arthragrostis
14. Calyptochloa
18. Chaetopoa
86. Tarigidia
94. Trachys

The Anthephora group is characterized by the terminal inflorescence branches terminating in a spikelet and disarticulation at the base of the primary branches. There is no character or combination of characters which makes a reasonable separation of this group into unique morphologically similar subgroups. Anthephora has the first glumes modified into hardened bristle-like structures. In addition to this unusual character, it is best separated from other taxa with a pronounced callus and adaxial spikelets. Similar glume modifications are found in *Chaetopoa*, which is distinguished within this group by a relatively thin textured upper floret. First glume encircling the base of the spikelets separates

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Arthragrostis, an Australian monotypic genus, from the other genera, as does the presence of a pronounced rachilla between the glumes. *Calyptochloa* is included in this group because of the secondary point of disarticulation at the culm nodes. It is most similar to the taxa of the *Melinis* group in which it shares the characteristic of primary point of disarticulation at the spikelet base. However, within this group *Calyptochloa* is best separated from the other genera on inflorescence form, type of ligule, presence of cleistogamous inflorescences, and

other significant characters. *Tarigidia*, an African monotypic genus, is best separated on the presence of a differentiated callus and secund primary inflores-cence branches. *Trachys* is unique in possessing a winged indurate lower lemma.

Isachne Group

22. Coelachne
 32. Heteranthoecia
 41. Isachne

45. Limnopoa 79. Sphaerocaryum

The Isachne group consists of those genera commonly placed in the Isachneae. This tribe is commonly defined on the basis of disarticulation above the glumes. However, this characteristic occurs within a number of genera of the Paniceae (see Brachiaria, Panicum and Yakirra). Point of disarticulation and differentiation of the pedicel apex is a combination of characters which separates this group. This complex of genera possesses in common persistent glumes after disarticulation and an undifferentiated pedicel apex. In the other members of the Paniceae where disarticulation occurs above the glumes the pedicel apex is consistently differentiated. Within this group texture of the fertile floret and number of fertile florets are the best characters for distinguishing genera. Coelachne has two fertile florets and a membranous upper floret. Heteranthoecia has a hardened fertile floret, two florets, and a panicle with racemose primary branches. Isachne has hardened florets and a panicle with spreading primary branches. Limnopoa is unique in possessing a true raceme inflorescence. Sphaerocaryum has one fertile floret which is relatively thin in texture.

Digitaria Group

Acritochaete
 Ancistrachne
 Anthaenantia
 Arthropogon
 Baptorhachis
 Cyphochlaena
 Digitaria

38. Hylebates
 39. Hymenachne
 47. Megaloprotachne
 50. Microcalamus
 68. Pseudechinolaena
 74. Sacciolepis
 78. Snowdenia

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# 34. Homolepis83. Stereochlaena35. Homopholis91. Thyridachne

The Digitaria group consists of those genera in which the branches terminate in a spikelet, disarticulation at the spikelet base, flat margins on the upper lemma, and the ligule a membrane or ciliate membrane. Within this complex, texture of the upper floret is the best character for initially separating the 18 genera into subgroups. Cyphochlaena and Arthropogon are unique within this group in having a hyaline upper lemma. Cyphochlaena can also be distinguished on the presence of heteromorphic spikelets. On other characters, principally spikelet shape, Cyphochlaena is similar to Cyrtococcum a member of the Panicum group. Arthropogon is unique in having a differentiated callus. Snowdenia is the only member of this group with exclusively a membranous upper floret but can also be distinguished on the basis of a raceme inflorescence and present first glume. A membranous to coriaceus upper lemma is characteristic of Hylebates, Hymenachne, Acritochaete, Anthaenantia, Baptorhachis and Stereochlaena. The best characters to separate Hylebates from other members of this subgroup include a pronounced rachilla between the glumes, an awned lower lemma, and spreading primary branches. The most similar genera to Hylebates is Acritochaete and Baptorhachis. Hymenachne is similar to Digitaria and Homolepis but can be separated on the presence of a rachilla pronounced between the glumes and first glume encircling the spikelet base. Acritochaete, an African monotypic, is similar to Stereochlaena and separated from the genera of the group by the presence of an awned second glume and lower lemma and oblique spikelets. Anthaenantia is similar to Digitaria and best separated within the group in lacking the first glume and having loosely arranged spikelets on the primary branches which are not distinctly secund. Baptorhachis, an African monotypic, is similar to Acritochaete but has a cleft and awned upper lemma and second glume. Stereochlaena, another African monotypic, also has an awned lower lemma but paired spikelets and lacks a main inflorescence axis. Remaining genera of this group have a cartilaginous to indurate upper floret. Megaloprotachne, Pseudechinolaena and Thyridachne are similar with a grooved lower lemma. Within this subgroup Megaloprotachne is unique in having a first glume not encircling the spikelet base. Pseudechinolaena has a pronounced rachilla between the florets whereas Thyridachne, an African monotypic, lacks this development. Sacciolepis is unique in having a saccate second glume and Ancistrachne has unicinate hairs on the second glume. Microcalamus, an African monotypic, has a pronounced rachilla between the florets and a differentiated apex on an indurate upper lemma. Digitaria, Homolepis and Homopholis are morphologically similar. Within this subgroup Homopholis has margins of the upper lemma with the same texture as the body. Digitaria is best separated from Homolepis on the basis of spikelet orientation. Digitaria is abaxial.

## Melinis Group

Alloteropsis
 Amphicarpum
 Anthaenantia
 Arthropogon
 Calyptochloa
 Chaetium

48. Melinis
49. Mesosetum
51. Mildbraediochloa
72. Reynaudia
73. Rhynchelytrum
75. Scutachne

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21. Cleistochloa 44. Lecomtella

93. Triscenia

The *Melinis* group consists of those taxa with the rachis terminating in a spikelet, disarticulation at spikelet base, upper lemma with flat margins, and the ligule a fringe of hairs. Included here are two genera, *Calyptochloa* and *Chaetium*, previously treated in the *Anthephora* group. *Anthaenantia* and *Arthropogon* also occurs in the *Digitaria* group but also need to be treated here. Within this generic complex the best character to separate among the genera is texture of the upper floret. Seven genera have an upper floret hyaline to membranous and 10 genera are chartaceous to indurate. Only two genera, *Lecontella* and *Rhynchelytrum*, overlap the subgroups.

The upper lemma is hyaline to membranous in Arthropogon, Lecontella, Melinis,

Mildbraediochloa, Reynaudia, Rhynchelytrum and Triscenia. Within this subgroup of similar taxa, Arthropogon is best distinguished by the presence of a differentiated callus and an awned first glume. Lecontella is the only and romonoecious genus of the subgroup but is also separated on the basis of differentiated upper lemma margins and an unawned first glume. Mildbraediochloa, an African monotypic, is unique within this group in having an awned upper floret. Reynaudia is the only genus consistently with two stamens but can also be separated on the basis of an undifferentiated callus and awned first glume. It is most similar to Arthropogon. Melinis and Rhynchelytrum are morphologically similar. They are similar in terms of the following significant sequence of characters which serve to separate them from other genera of this subgroup; plants hermaphroditic, inflorescence a panicle, primary branches spreading, first glume present, first glume muticous and upper lemma muticous. They are best separated on the basis of arrangement of the primary inflorescence branches. In Rhynchelytrum the primary branches are secund or distichous. It is interesting to note that all the genera of this subgroup have lateral compression of the spikelets except Triscenia which is dorsiventrally compressed.

The upper lemma is chartaceous to indurate in Alloteropsis, Amphicarpum, Anthaenantia, Calyptochloa, Chaetium, Cleistochloa, Lecomtella, Mesosetum, Rhynchelytrum and Scutachne. Two Australian genera Calyptochloa and Cleistochloa and the North American Amphicarpum possess cleistogamous inflorescences.

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Within these three genera *Calyptochloa* is distinguished by an awned upper floret. Amphicarpum is best separated from Cleistochloa on the location and morphology of the cleistogamous spikelets. In Amphicarpum they are subterranean and morphologically different from the chasmogamous spikelets. Alloteropsis and *Chaetium* differ from the remaining taxa in the presence of an awned upper floret and best separated from each other due to the oblique spikelet base in Chaetium. Remaining genera of this subgroup include Anthaenantia, Chaetium, Lecontella, Mesosetum, Rhynchelytrum and Scutachne. Anthaenantia is the only genus of this subgroup lacking a first glume. Lecontella is the only and romonoecious genus and also the only C-3 genus. A raceme inflorescence is found exclusively in Mesosetum. Chaetium, in which the upper floret may be unawned, is unique in this last subgroup of six genera in having a flat pedicel apex. Unique significant characteristics of Rhynchelytrum within this subgroup include the presence of secund or distichous primary branches and loosely arranged spikelets. Scutachne is unique within this group with the first glume completely encircling the spikelet base.

## Panicum Group

- Acroceras
   Anthaenantiopsis
   Arthragrostis
- 46. Louisiella 4. Oplismenopsis 5. Oplismenus

 9. Artificagrosits
 9.

 11. Axonopus
 57.

 16. Centrochloa
 8.

 24. Cyrtococcum
 9.

 29. Echinolaena
 4.

 31. Eriochloa
 66.

 33. Holcolemma
 67.

 36. Hydrothauma
 80.

 40. Ichnanthus
 88.

 43. Lasiacis
 89.

Oplismenus
 Otachyrium
 Ottochloa
 Panicum
 Panicum
 Paspalum
 Plagiantha
 Poecilostachys
 Spheneria
 Thrasya
 Thrasyopsis

The *Panicum* group consists of genera having in common the branches terminating in a spikelet, disarticulation at spikelet base, upper lemma with involute margins, and the ligule a membrane or ciliate membrane. As in previous groups, INTKEY analysis indicated that texture of the upper floret is the best or most significant character to initially separate among the genera of the group. Eight genera possess a hyaline to chartaceous upper floret. These include *Anthaenantiopsis*, *Cyrtococcum*, *Hydrothauma*, *Louisiella*, *Oplismenopsis*, *Otachyrium*, *Plagiantha* and *Poecilostachys*. *Anthaenantiopsis* is the only member of this subgroup with a flat to convex pedicel apex. It is also the only member with the palea of the upper floret not enclosed at the apex. *Cyrtococcum* is unique with a crested differentiated apex on the upper lemma. In addition, it has lateral compression

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of the spikelets and quaquaversal primary inflorescence branches. Cyrtococcum is similar to Poecilostachys which also has lateral spikelet compression. Poecilostachys differs from *Cyrtococcum* on the absence of a differentiated upper lemma apex. Hydrothauma, an aquatic monotypic genus from Africa, is the only member of this subgroup with abaxial spikelets. Leaf blades of Hydrothauma are unique within the Paniceae due to the development of sinuous longitudinal lamallae on the adaxial surface of the leaf blades. Louisiella, a monotypic genus from Africa, is the only member of this subgroup with a relatively short upper floret (0.5 - 0.6 times)spikelet length). It can also be distinguished on the first glume encircling the spikelet base and growing in hydrophytic habitats. Oplismenopsis, a South American monotypic, also grows in water and the only member of this group with an awned second glume. Otachyrium, a South American genus of about seven species, also grows in wet habitats and has three characteristics of equal significance which are unique within this subgroup. It is the only member with a dense textured lower lemma, the nerves of the lower palea developed into lateral wings, and lower lemma hyaline in the central area. Plagiantha, another South American monotypic, is most similar to Otachyrium and best separated from this genus due to the presence of a differentiated apex on the upper lemma. The second subgroup within the Panicum group consists of the remaining taxa and defined on the basis of a cartilaginous to indurate upper floret. Two genera, Cyrtococcum and Otachyrium, overlap between the subgroups. Within this second subgroup of nineteen genera the best separating character is whether the genera are C-3 or C-4. C-4 genera include Axonopus, Centrochloa, Eriochloa, Holcolemma, Panicum, Paspalum, Spheneria, Thrasya and Thrasyopsis. The first glume fused with the callus to form a distinct cup-like structure is only found in Eriochloa. Partial fusion of the first glume is found in Thrasya. Spheneria, a South American monotypic, is the only genus with an oblique attachment of the pedicel and spikelet base. Once Spheneria is excluded, Paspalum becomes the only genus with abaxial spikelet orientation. Axonopus is most similar to Thrasya and best separated from members of this subgroup in lacking the first glume, adaxial spikelets, callus undifferentiated, and absence of the central groove on the lower lemma. Centrochloa, a South American monotypic, is very similar to Axonopus and differentiated on the presence of a short blunt callus and the extension of the second glume into a long point or spur. Holcolemma is included in this group due to its variation in the presence of absence of a bristle. Overall, it is most similar to members of the Setaria group. Here, it is separated on the basis of the rugose upper floret and the first glume not fused as in Eriochloa. Paspalum is best separated due to abaxial spikelets and a flat to convex pedicel apex. It is most similar to Thrasya. Thrasya and Thrasyopsis possess in common a hyaline area in the central part of the lower lemma. They are best separated from each other on the number of second glume

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nerves and texture of the florets. *Panicum* is distinguished from these genera in lacking the characters or combination of characters used to define the other genera.

C-3 genera include Acroceras, Arthragrostis, Cyrtococcum, Echinolaena, Ichnanthus, Lasiacis, Oplismenopsis, Oplismenus, Otachyrium, Ottochloa and Panicum. Within this subgroup Acroceras, Arthragrostis, Echinolaena, Ichnanthus and Panicum have the rachilla pronounced between florets. Ichnanthus and to a limited degree Echinolaena

is unique in possessing pronounced basal scars or appendages associated with the rachilla and upper floret base. Arthragrostis has a relatively long and filiform rachilla. Acroceras is separated within this subgroup in having a differentiated apex of the upper lemma. Echinolaena is unique with the pedicel apex flat and not concave. Panicum lacks those characteristics used to define the other genera. Genera lacking the pronounced rachilla between florets include Acroceras, Cyrtococcum, Lasiacis, Oplismenopsis, Oplismenus, Otachyrium, Ottochloa and Panicum. Acroceras, Cyrtococcum, Lasiacis are differentiated at the apex and separated on the basis on spikelet compression. Lasiacis has terete spikelets, Cyrtococcum laterally compressed spikelets, and Acroceras dorsiventrally compressed. An undifferentiated upper lemma apex and an awned first glume separates Oplismenopsis and Oplismenus which are distinguished on the first glume encircling the spikelet base in Oplismenopsis. Otachyrium is the only member of this subgroup with a hyaline area on the central part of the lower lemma. Ottochloa is the only member of this subgroup with abaxial spikelets but also has equal glumes shorter than the spikelet.

## Paspalum Group

Alloteropsis
 Anthaenantiopsis
 Axonopus
 Brachiaria
 Brachiaria
 Calyptochloa
 Eccoptocarpha
 Echinochloa
 Echinolaena
 Echinolaena
 Entolasia

56. Oryzidium
 64. Paspalum
 85. Streptostachys
 87. Tatianyx
 89. Thrasyopsis
 95. Tricholaena
 97. Urochloa
 98. Whiteochloa
 100. Yakirra

# 31. Eriochloa 101. Yvesia40. Ichnanthus

The *Paspalum* group is characterized by the rachis terminating in a spikelet, disarticulation at the spikelet base, margins of the upper lemma enrolled, and the ligule a fringe of hairs are absent. A number of these genera overlap with previously defined groups but are best discussed here to show the overall similarity within the tribe. There are no characters which make a suitable separation of these

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21 genera into large subgroups. Entolasia and Streptostachys have a hairy upper floret and are best separated by the rachilla pronounced between the florets in Streptostachys. Eriochloa is unique with the fusion of the first glume and callus. Seven of the remaining 18 genera have a pronounced rachilla between the florets. These include Calyptochloa, Eccoptocarpha, Echinolaena, Ichnanthus, Oryzidium, Whiteochloa and Yakirra. Ichnanthus and to a limited degree Echinolaena is unique in possessing pronounced basal scars or appendages associated with the rachilla and upper floret base. These genera are best distinguished by the rachilla being curved in Ichnanthus. Whiteochloa is the only member of this subgroup with lateral spikelet compression. Only Calyptochloa has an awned first glume. Eccoptocarpha best separates from other members of this subgroup on the basis of the saccate second glume. Oryzidium is unique in having an awned lower lemma. Finally, Yakirra is most similar to Ichnanthus but separates due to the swollen rachilla. Of the remaining 11 genera only Urochloa has a rugose upper floret. Of the remaining 10 genera only Alloteropsis has an awned upper floret. Of the remaining 9 genera only Tatianyx and Tricholaena have spreading primary inflorescence branches and these are best separated by the oblique spikelet base in Tatianyx. Tricholaena is also similar to members of the Melinis group. Remaining seven taxa are best separated on differentiation of the pedicel apex. Anthaenantiopsis, Paspalum, Thrasyopsis have a flat to convex pedicel apex. Paspalum is the only member of this group with abaxial spikelet orientation. Thrasyopsis best separates from Anthaenantiopsis on the basis of the coarse texture lower lemma. Of the remaining four genera only Echinochloa has a differentiated upper lemma. A first glume is present only in Brachiaria. Axonopus and Yvesia are best separated on the absence of the lower palea in Axonopus. Information presented by this analysis groups similar genera on the basis of the best shared significant characteristics. Axonopus and Yvesia are the last genera treated from the initial group of 102 taxa. These genera have in common the following sequence of characters; the rachis terminating in a spikelet, disarticulation at spikelet base, margins of upper lemma enrolled, ligule a fringe of hairs, a glabrous upper floret, first glume not fused with callus, rachilla not pronounced between florets, upper floret not rugose, upper floret not awned, appressed secondary branches, a concave pedicel apex, upper lemma not differentiated at apex and the first glume absent.

#### ADDITIONAL SIGNIFICANT CHARACTERS

Characters used in the analysis of the previous two sections were selected on the basis of an assessment of character reliability and the variation among the genera. Thirty-nine characters are used and discussed in the section describing the distribution of characters in the diagnostic descriptions. These characters and many others are used in the analysis and discussion of similarities among the

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genera. There are a number of additional potentially important characters not used in either section due to the presence of more significant characters or by the relatively low reliability initially assigned to the character. The objective of this section is to briefly discuss these characters and to describe the value of the characters within the tribe.

Twenty-four of the genera are exclusively annual and 43 are exclusively perennial. The remaining 35 genera are variable. This character is important only for separating genera with a low number of species. Specifically, the 67 genera which are either annual or perennial are monotypic or contain a very few number of species. Most of the variable genera possess a relatively large number of species. Whether the culm internodes are hollow, spongy or solid has limited value. Nine genera are exclusively solid, 12 are exclusively spongy, and 57 are hollow only. Presence of spongy internodes is correlated with the occurrence in aquatic or semi-aquatic habitats. Viscid internodes are exclusive to Melinis and two genera, Lecontella and Tarigidia are exclusively glaucous. Twenty-six genera possess species with viscid or glaucous internodes. Leaves are exclusively distichous only in Chamaeraphis; however, distichous leaves can occur in eight genera (Chamaeraphis, Isachne, Limnopoa, Paspalum, Pseudoraphis, Reimarochloa, Spinifex and Stenotaphrum). Ovate leaf blades are exclusive in Sphaerocaryum. Most of the genera (94) have filiform to linear blades. Four genera (Calyptochloa, Microcalamus, Plagiantha and Streptolophus) have lanceolate blades. Whether the inflorescence is enclosed in the leaf sheath has limited taxonomic value. The inflorescence of all species of Spinifex and Thuarea are totally enclosed in sheaths. Some species of Axonopus, Pennisetum and Zygochloa have completely enclosed inflorescences. Partially enclosed inflorescences occur in 32 genera but is exclusive in Lecontella, Louisiella and Odontelytrum. Most of the genera (95) have species with fully exerted inflorescences. A distinctly wavy inflorescence main axis is characteristic of Anthephora and Chamaeraphis. Width of the primary inflorescence branch greater than 5 mm occurs in some species of Chlorocalymma, Streptolophus, Thrasya and Thrasyopsis. In the remaining genera the primary branch is less 5 mm wide. Bristles are distinctly flattened in all species of Chlorocalymma and Uranthoecium. Other genera with flattened bristles include Cenchrus, Odontelytrum and Paractaenum. Branched bristles occur in Chlorocalymma, Odontelytrum, Paractaenum and Streptolophus. Remaining bristle bearing genera possess

unbranched bristles.

Whether the spikelets occur solitary or paired has limited value. Sixty-eight genera are exclusively solitary and eight genera have only species with paired spikelets. Remaining genera are variable or not applicable for this character. Length of the first glume has limited diagnostic value for the genera; however, it becomes important when used relative to the length of other structures. Of the 95 genera possessing a first glume, 62 genera have a first glume 0.1 to 0.7 times the length of the second glume. Thirty-five genera have a first glume more than

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0.7 times the second glume. There is an overlap of one genus. Perhaps this is somewhat misleading since the length of the first glume awn (when present) is included in the results. The best separation for the relative length of the first glume and spikelet length is at 0.5. Sixty genera are in the range of 0.1 to 0.5 and 43 in the range of 0.6 to 1.0. The best separation for the relative length of the second glume and spikelet length is at 0.7 to 0.8. Thirty-five genera fall into the range of less than 0.8 and 74 genera fall in the range of 0.9 to 1.0.

Presence of obvious transverse nerves on the lemma of the lower floret is found in Eccoptocarpha and also found in some species of Paspalidium and Urochloa. Relative length of the upper and lower florets has limited diagnostic value. Eleven genera have some taxa in which the upper floret is less than 0.5 times spikelet length and 94 genera have taxa with the upper floret greater than 0.5 times spikelet length. Diagnostic value of whether the lemma of the floret is shiny or dull is frequently underestimated. A shiny upper lemma is found in all species of Brachiaria, Dissochondrus, Eccoptocarpha, Echinolaena, Homopholis, Hydrothauma, Oplismenopsis, Oplismenus, Oryzidium, Otachyrium, Paratheria, Poecilostachys, Pseudechinolaena, Pseudoraphis, Sacciolepis, Tatianyx and Tricholaena. Seventy-eight genera have species in which the upper lemma is always dull. An overlap of seven genera exists for this character. For the 49 genera in which the margins of the upper lemma are flat, 20 have a relatively thin margin and 23 a margin of the same texture as the body. There is an overlap of six genera for this character.

#### SUMMARY

This paper presents a detailed discussion of the significance and application of characters in defining the taxonomy of the recognized genera of the Paniceae. Retrieval of this information was possible due to the application of the DELTA system. Traditional approaches do not provide the types of conclusions discussed in the preceding text. It was found that 39 characters were required to provided diagnostic descriptions for the 102 genera. A diagnostic description was given for each genus. When the full range of variation within the tribe is considered, these are the characters which in reality delineate the genera. Selection of these characters was determined by the variation within the genus and by the variation among the rest of the genera. If for some reason the definition of a genus were to change, this change would effect the definition of other genera within the tribe. The number of characters required to distinguish individual genera varied from two to fourteen and was dependent on how variable the genus was on significant characters. It was proposed that the relative significance of a character could be determined by the number of times that a character was required in the diagnosis. A detailed discussion is provided on the distribution of significant characters among the genera. These 39 characters include the following which are not listed in order of significance. Three general characters were plant sexuality, branching pattern of the vegetative axis, and ligule type. Eleven inflorescence characters

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include the type, arrangement of primary branches, orientation of secondary branches, degree of reduction of branches, arrangement of branches, presence of bristles, differentiation of pedicel apex, shape of pedicel apex, angle of disarticulation of pedicel apex, depression of pedicel apex, and point of disarticulation. Presence of a cleistogamous inflorescence was important in a limited number of genera. Three general spikelet characters were presence of heteromorphic spikelets, orientation of spikelets, and spikelet compression. Five first glume characters include presence or absence, presence of a callus, whether encircling the base, whether the base is inflated, and presence of an awn. Development and shape of a rachilla were included. Two second glume characters include presence and shape. Number of fertile florets was found to be significant. Three lower floret characters include texture, presence of a central groove, and presence of a hyaline area. Six upper floret characters include texture, shape of the margins, presence of hairs, ornamentation, basal modifications, and presence of an awn. Genera were grouped based on the presence of shared significant characters. Point of disarticulation and whether bristles were present or absent were found to be the most significant characters and were used to make the initial separation of the genera into groups. Similarities within the groups were discussed using the next most significant characters. Recognized groups include the Cenchrus, Setaria, Anthephora, Isachne, Digitaria, Melinis, Panicum, and Paspalum. This study together with phenetic and cladistic studies will provide the basis from which a

classification of the tribe will be produced.

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